BREVIORA

Museum of Comparative Zoology

Cambridge, Mass. 31 December, 1968 Number 309

VARIABILITY OF RODENT INCISOR ENAMEL AS VIEWED IN THIN SECTION, AND THE MICROSTRUCTURE OF THE ENAMEL IN FOSSIL AND RECENT RODENT GROUPS

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Abstract. The microstructure in enamel of various fossil and Recent rodent incisors is described from thin sections. Measurements of enamel thickness and inclination of bands in the inner enamel layer were made from sagittal sections on large and small samples of *Rattus norvegicus* and on small samples of the Eocene forms *Paramys copei* and *Knightomys depressus*. Statistical analyses of these data show that a sample of size 10 yields an adequately close approximation to the population mean. Differences in enamel dimensions between upper and lower incisors and between incisors of different species are apparent. Thickness and inclination can be used in the identification of isolated incisors when data for other rodents have been compiled. Band width is of apparently similar utility, but small size precludes anything more than rough measurement at 430 diameters magnification. Korvenkontio's "external index" and other measurements taken from sagittal sections are deemed unreliable. Rodent species whose enamel has been studied are listed according to the kind of enamel they possess. Pauciserial enamel, found only in Eocene and Oligocene forms, appears to be the structural predecessor of uniserial and multiserial enamels, which occur in all post-Oligocene rodents examined. At present, the microstructure of incisor enamel is useful as an additional character for determining the systematic position of rodent higher taxa, but it is no touchstone.

INTRODUCTION

That incisor enamel may be useful in the classification of rodents was first suggested by the work of Tomes (1850) and later by that of Korvenkontio (1934). Tomes examined the microstructure of incisor enamel in a number of living rodents and found that within supposedly related groups the arrangement of enamel prisms is similar; his descriptions and figures showed that the enamel of modern rodents is of two basic kinds. Korvenkontio named these uniserial and multiserial. His extension of the research to other

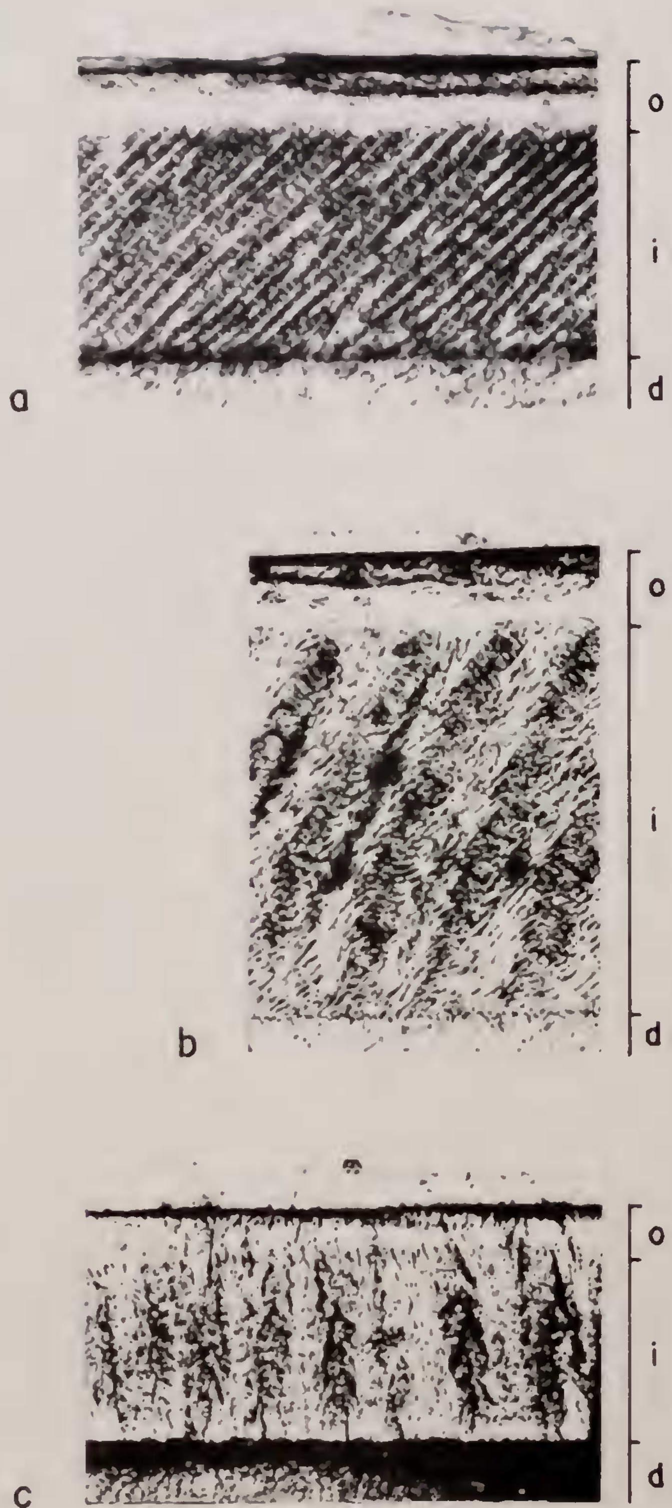

Figure 1. Sagittal sections of enamel in lower incisors: a. *Rattus norvegicus;* b. *Metaphiomys schaubi;* c. *Paramys copei.* Tips of incisors are to the right. Magnification is approximately 240 diameters. Abbreviations: o, outer enamel layer; i, inner enamel layer showing bands; d, dentine.

modern rodents and to various fossil forms greatly enlarged Tomes' work and led to the discovery of a third kind of incisor enamel structure, which he named pauciserial, among early fossil forms. In all rodents enamel covers the outer, labial side of the incisors; it may extend slightly on the mesial and distal sides.

Korvenkontio published an extensive table (1934: 116-123) giving the dimensions of various parts of the enamel and indices derived from these measurements for the incisors of all the species he examined. These suggested the possibility that some dimensions and ratios, at least, might be characteristic of low level taxa. If this should prove to be true, it would be a relatively simple matter to section, measure, and identify fossil rodent incisors, which are so frequently found separated from their jaws. Korvenkontio states (1934: 125, footnote) that in his study of 72 Recent and 33 fossil forms he used about 520 sections. He attempted to make sagittal, transverse, and frontal sections of each species wherever possible, and thus his sample size for measurement was very small.

The primary purpose of the work here reported has been to determine the variability of enamel and the sample size needed to obtain meaningful measurements. In the course of the work I have had occasion to section incisors of a number of rodents, both Recent and fossil. These are included in Table 5, which lists all species whose incisor microstructure is known.

THE KINDS OF RODENT INCISOR ENAMEL

A sagittal section of *uniserial* enamel, for example that of *Rattus norvegicus* (Fig. 1a), reveals two layers of enamel. The inner layer in this aspect appears to consist of bands one enamel prism wide that extend outward from the dentine and upward toward the tip of the tooth. On close examination each band is seen to be divided into small units, somewhat like a string of beads. Study of transverse and frontal sections reveals that each band is the cross-sectional view of a transverse lamella of enamel prisms. The width of bands and prisms is the same in sagittal section; Korvenkontio's data show a range of 2.2 to 5.0 microns for uniserial enamels. The prisms in a single lamella are parallel; they do not make a right angle with the dentine but are at some oblique angle to the sagittal plane of the tooth. A band is, therefore, the cross-section of prisms comprising a lamella. The prisms of every other lamella have the same orientation. There are two kinds of differences in orientation of prisms of adjacent lamellae. In transverse section the prisms of adjacent lamellae are seen to cross each other at a fairly constant angle. Frontal sections reveal that the prisms are

tilted to one side of the sagittal plane in every other lamella and to the other in the alternating set. In the outer layer of the enamel the prisms of all lamellae are parallel, and lamination ceases; they are usually inclined more steeply toward the tip of the tooth than in the inner layer.

A sagittal section of *multiserial* enamel, for example that of *Metaphiomys schaubi* (Fig. 1b), also reveals two layers of enamel. The bands of the inner layer are many prisms wide. Korvenkontio found that band widths range from 12 to 30 microns for multiserial enamels. Prisms are directed obliquely with respect to the direction of the bands; the obliquity differs in adjoining bands but corresponds in alternate ones. Prisms of the outer layer are parallel and more steeply inclined toward the tip of the tooth, as in uniserial enamels. The three-dimensional structure is more complicated than in uniserial enamels, and for my own work I have relied on Tomes' description (1850: 552-53), which I paraphrase closely here: In an oblique transverse section parallel with the course of the enamel lamellae, the inner enamel layer looks as though the prisms were thrown into waves, the furrows of which commence at the surface of the dentine and, proceeding obliquely outwards, crop out where the prisms become parallel in the external layer. The prisms pursue a serpentine course in the inner, lamelliform portion, where they describe tolerably uniform curves. By altering the focus of the microscope it may be seen that the prisms of adjacent layers pursue a similar serpentine course, but are arranged so that the concavities and convexities point in opposite directions, thus producing a sort of figure 8.

Pauciserial enamel, for example that of *Paramys copei* (Fig. 1c), is also divided into two layers. The prisms of the inner layer may or may not be organized into lamellae. In a sagittal section the bands of lamellar enamel are seen to be of somewhat variable width, depending on the number of prisms included. Korvenkontio found that band widths of pauciserial enamels fall between 5 and 16 microns, between the ranges for uniserial and multiserial enamels, with slight overlap. The structure appears similar to multiserial enamel but lacks the uniformity of organization. Bands are usually not inclined. Prisms in the external portion are slightly inclined toward the tip of the tooth, though this is not visible in the figure. Some pauciserial enamels have fewer prisms per band, and thus the bands are narrower, suggesting uniserial enamel in appearance.

These descriptions of the kinds of enamel seen in sections of rodent incisors refer only to the vicinity of the midline of the

tooth, where the structure is clearly seen. The terms uniserial, multiserial, and pauciserial apply, of course, to the inner layer of the enamel only.

MEASUREMENTS AND INDICES

Sagittal sections are the best for determining what kind of enamel is present in a given rodent incisor, and they are the easiest to make; therefore, I have considered only measurements made from them.

Total enamel thickness and thicknesses of the two enamel layers can be measured. Korvenkontio's external index, which is the percentage of total enamel thickness occupied by the outer layer, compares these dimensions. Total enamel thickness is defined as the length of a line segment normal to the enamel surface at a point, in the vicinity of the midline of the tooth, at which the enamel is thinnest. If a sagittal section contains this segment, it occurs where the enamel is unworn and thinnest. The geometry of rodent incisor enamel distribution, as seen in transverse section (Fig. 2a and b), makes underestimation of the total enamel thickness impossible in a reasonably good section.

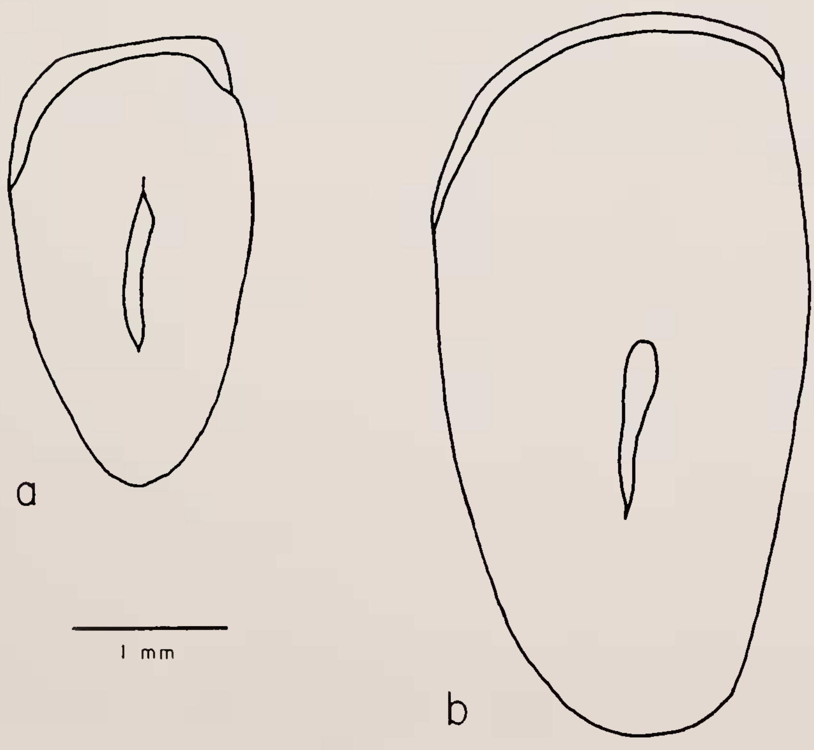

Figure 2. Transverse sections of upper incisors: a. *Rattus norvegicus;* b. *Paramys copei.* Mesial side is to the right.

Band width and inclination of bands are also measured best in sagittal section. Korvenkontio defined inclination as the angle at which bands intersect a perpendicular to the dentine in the sagittal plane.[1] When bands appear curved, a tangent to the midpoint of a band is used to determine inclination. Prisms in the external layer also have an inclination that can be measured; this is not visible in most sections, however, and I have not considered it. In this paper I use enamel thickness, external index, band width, and inclination in the internal enamel layer according to Korvenkontio's definitions for sagittal sections.

MATERIALS

Incisors of 48 individuals from a highly inbred strain of albino *Rattus norvegicus* were available to me at the beginning of this project. This is a large sample for statistical analysis by paleontological standards. The heads had been preserved in formaldehyde, and sexes were not recorded. Incisors of *Paramys copei* and *Knightomys depressus* were also available in fair quantity. These had been collected by Amherst College parties from the early Eocene Lysite member of the Wind River Formation in the Wind River Basin, Wyoming. Individual incisors from a variety of rodents were also sectioned; specimens were obtained from the collections of Amherst College, Albert E. Wood, the Museum of Comparative Zoology, the University of Texas, and the Yale Peabody Museum.

PROCEDURE

Standard sectioning techniques were used. All four incisors from each rat were sectioned on one petrographic slide. Fossil incisors and individual modern incisors were sectioned singly. Preliminary grinding was done on a water-bathed 600 grain diamond wheel that turned at approximately 100 rpm. Sections were hand held. Final polishing was done with wet 900 grain alundum on wood, and then sections were etched briefly with dilute hydrochloric acid; this step makes the enamel structure visible. When sections of modern teeth become thin, water absorption causes them to buckle. This difficulty was solved by drying the section before it became thin and then impregnating it with mineral oil which acts as a waterproofing agent.

[1] Tomes (1850) measured inclination as the angle made by bands and the dentine surface.

Thickness measurements were made by comparing the projection of a thin section with a micrometer slide. The number of bands within a standard unit of a micrometer eyepiece divided by the length of the unit in millimeters yields the average band width. Inclination was measured on the rotating stage of a petrographic microscope. In each case 430 diameters magnification was used.

Tabulation and statistical analyses of the measurements are given in Tables 1-4. The formulae used in computation are those given by Simpson, Roe, and Lewontin (1960: 84, 90, 166). Abbreviations are as follows: N, sample size; OR, observed range;

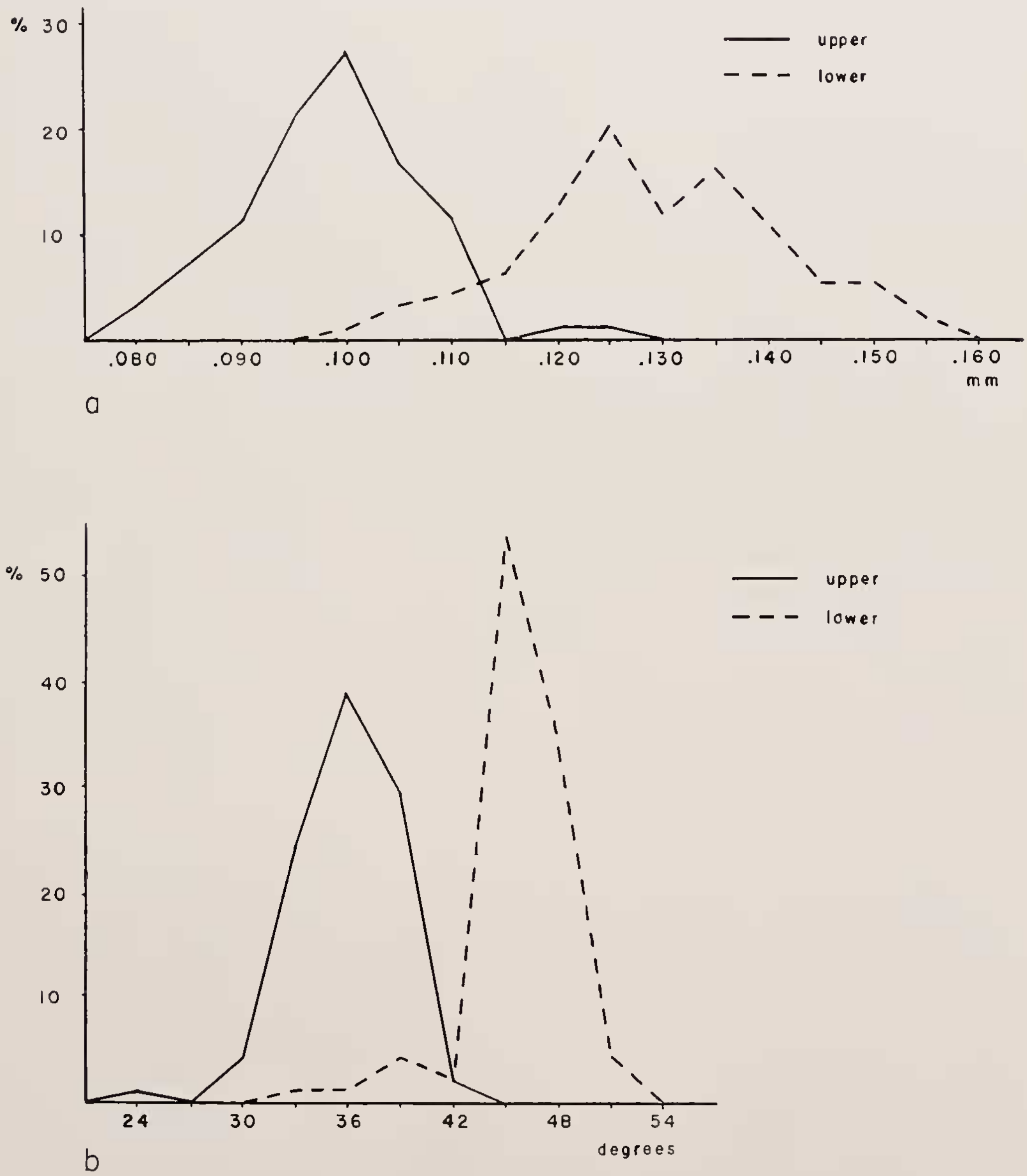

Figure 3. Frequency distributions for incisors of *Rattus norvegicus*: a. total enamel thickness; b. enamel prism inclination.

$\overline{X}$, arithmetic mean; Conf. Int., confidence interval of the mean; SD, one standard deviation unit; V, coefficient of variation. In all thickness measurements there is an error in estimation of ±.001 mm; this error is inherent in the mean. Frequency distributions for enamel thickness and inclination of bands in the large sample of albino laboratory rats appear in Figure 3a and b.

Although all four incisors of forty-eight rats were sectioned, not all individual sections were usable, and thus the sample size varies slightly. Inclination was not measured in *Paramys copei* and *Knightomys depressus* because prism bands are not well defined and are nearly perpendicular to the dentine surface. The sample size in both cases was too small for frequency diagrams to be constructed. Measurements of band widths were, at best, crude, because boundaries are not well defined and magnification was low for such small objects. Consequently, I present only average width and range under the appropriate headings.

TABLE 1

Data for albino laboratory rat incisors.

Incisor	N	OR	$\overline{X}$	95% Conf. Int.	SD	V
Total enamel thickness (in mm)						
Upper	96	.080-.126	.099	±.002	.009	8.7
Lower	93	.100-.155	.129	±.003	.012	9.1
Inclination of enamel prisms (in degrees)						
Upper	95	23-42	36	±.6	3	8.3
Lower	93	32-51	46	±.6	3	6.1

DESCRIPTION OF SAMPLES

Rattus norvegicus (*laboratory strain*). The incisor enamel is uniserial (Fig. 1a), and the enamel thickness is greater in the lower than in the upper incisors of each individual rat, although the ranges of total enamel thickness for upper and lower incisors overlap appreciably (Table 1). In only one specimen were the measurements within the error of estimation of each other, the enamel thickness of the upper right incisor being .126 mm and of the lower left, .127 mm. The overlap of ranges shows that it is unsafe to decide whether upper or lower incisors have the thicker enamel on the basis of only one or two specimens. The frequency distribution is graphed in Figure 3a.

The 95 per cent confidence interval for the mean is quite small in relation to the total thickness. The standard deviations are greater for lower incisors than for uppers. The coefficients of variation are high for a Recent species (Simpson, Roe, and Lewontin, 1960: 92). This may be accounted for by deviation of the section from the sagittal plane and also by natural variation, such as effects of age, sex differences, and inbreeding, none of which can be excluded as a factor contributing to a high V. The distribution of enamel on the front of an upper incisor as seen in transverse section (Fig. 2a) is uneven; thus, deviation of sections from the sagittal plane could be the cause of considerable variation in thickness measurements. The enamel distribution is more uniform in lowers. Separate analysis of left and right incisors yielded the same mean in lowers and a difference of means in uppers that is within the estimated range of observational error.

The number of incisors of a single extinct species collected from one locality is usually small, on the order of ten or so. To test the reliability of enamel thickness measurements for small samples, I considered the data for forty-eight rats as representing an entire population with a known mean and took from it ten random samples of ten upper and of ten lower incisors. The results of the analyses are presented in Table 2. Although the means of these samples may be as much as five thousandths of a millimeter from the mean of the population, the ninety-five per cent confidence intervals of the means for all but one sample (upper incisors, sample 8) include it. This same sample has both the highest mean thickness and the least variability. With any two samples representing upper and lower incisors, the relative difference in enamel thickness is apparent; the smallest difference in mean enamel thickness obtainable from these results amounts to .020 mm and the largest is .039 mm.

Attempts to measure the thickness of either layer of the enamel separately were unsatisfactory, because there is no clear line of demarcation between the two. Figure 1 shows how bands of the inner layer project into the outer; it is impossible to establish a definite line that is consistently placed in each thin section. In the sample the outer enamel layer occupies *approximately* 30 per cent of the mean total thickness in uppers and 19 per cent in lowers. The observed ranges are 20 to 39 per cent for uppers and 14 to 27 per cent for lowers. In two individuals the external index of an upper and a lower incisor is the same, but in no instance in an individual is that of the lower greater. A regression analysis of these measurements of outer layer thickness versus total enamel

TABLE 2

Variability of total enamel thickness (in mm) in ten samplings, each of ten incisors selected at random from data for albino laboratory rats.

Samp.	OR	$\bar{x}$	95% Conf. Int.	SD	V
Upper incisors					
1	.085-.120	.101	±.007	.010	9.9
2	.080-.126	.099	±.009	.013	13.1
3	.085-.110	.097	±.006	.008	8.2
4	.085-.110	.099	±.005	.007	7.1
5	.092-.109	.099	±.004	.006	6.1
6	.094-.106	.100	±.003	.004	4.0
7	.080-.112	.095	±.006	.009	9.5
8	.100-.107	.104	±.001	.002	1.9
9	.085-.126	.102	±.009	.013	12.7
10	.092-.110	.101	±.004	.006	5.9
Lower incisors					
1	.110-.155	.129	±.011	.015	11.6
2	.119-.153	.134	±.008	.011	8.2
3	.110-.143	.127	±.007	.010	7.9
4	.107-.143	.128	±.007	.010	7.8
5	.111-.138	.127	±.007	.010	7.9
6	.114-.153	.129	±.008	.011	8.5
7	.111-.145	.124	±.007	.010	8.1
8	.107-.150	.131	±.011	.015	11.4
9	.107-.138	.126	±.008	.011	8.7
10	.110-.145	.129	±.008	.012	9.3

thickness was carried out within upper and lower incisors of the entire sample. The correlation coefficient for upper incisors is .27; for lowers, .18. This is extremely poor, but the gross difference between uppers and lowers remains.

Band width in sagittal section appeared nearly invariable at 450 diameters magnification. It is .0033 for both upper and lower incisors. The mean inclination of enamel prisms in the inner layer is distinctly greater in nearly all lower incisors (Table 1, Figure 3b). However, in one specimen the inclination of bands in one lower incisor was less than that of the uppers; in another, an upper and a lower incisor yielded the same angle. Thus, two teeth, even

from the same individual, may not indicate the usual relationship. The standard deviation of inclination is the same for both upper and lower incisors.

TABLE 3

Data for *Paramys copei* incisors.

Total enamel thickness (in mm) Incisor	N	OR	$\bar{x}$	95% Conf. Int.	SD	V
Upper	16	.088-.115	.104	±.004	.008	7.7
Lower	24	.065-.105	.088	±.004	.009	10.2

Paramys copei. The sample of incisors of *Paramys copei* from the Lysite represents a minimum of twelve individuals, all but two of the teeth being from the same locality. Enamel is pauciserial. In this species the distribution of enamel across the face of the tooth as seen in transverse section is fairly even (Fig. 2b). The error caused by the deviation of a section from the mid-plane is therefore not large when compared to the same situation in rat incisors.

The data presented in Table 3 indicate that the mean enamel thickness in upper incisors is .016 greater than in lowers, the reverse of the situation in rats. There is overlap in ranges, and examination of only a few teeth could show the opposite relationship. The standard deviations for upper and lower incisors are similar to the figure for upper incisors of rats. The sample is too small to construct a meaningful frequency distribution curve.

The mean band width and observed range are .017 mm and .013-.021 mm in upper incisors and .016 mm and .014-.023 mm in lowers. Inclination of bands is approximately zero. In any individual tooth, bands may be slightly inclined toward or away from the tip.

TABLE 4

Data for *Knightomys depressus* incisors.

Total enamel thickness (in mm) Incisor	N	OR	$\bar{x}$	95% Conf. Int.	SD	V
Upper	13	.103-.150	.120	±.009	.016	13.3
Lower	6	.053-.095	.068	±.005	.005	7.35

Knightomys depressus. The sample of *Knightomys depressus* from the Lysite represents a minimum of seven individuals. Enamel is pauciserial. The data presented in Table 4 show that the mean

enamel thickness is much greater in upper incisors and that the ranges for upper and lower incisors do not overlap. The lack of overlap may simply mean that the sample size is too small. The confidence interval, standard deviation, and coefficient of variation for the lower incisors seem low with regard to these figures for the other samples. They are in best agreement with those for small samples of rat upper incisors.

The distribution of enamel is similar to that in *Paramys copei*. The mean band width and observed range are .014 mm and .012-.017 mm in upper incisors and .012 mm and .009-.016 mm in lowers. Inclination of bands is approximately zero, and the boundary between inner and outer layers of enamel is again not a distinct line.

SAMPLE SIZE AND THE UTILITY OF MEASUREMENTS AND INDICES AS CRITERIA FOR IDENTIFICATION OF ISOLATED INCISORS

A sagittal thin section of a rodent incisor is sufficient to show whether the enamel is pauciserial, uniserial, or multiserial. A few sections provide a rough measure of enamel thickness. A sample of ten or more upper and ten or more lower incisors yields a mean enamel thickness with a fairly small confidence interval and shows the relationship of thicknesses. A sample of about a hundred individual upper and lower incisors is needed for graphing a frequency distribution of thickness. The inclination of bands in the inner enamel layer also yields a continuous curve when plotted for a sample of this size. The inclination of prisms in the external layer is usually not visible. A rough measure of band width may be made at a magnification of 430 diameters, but variation is not apparent.

The boundary between internal and external enamel layers is not a line, and thus the thickness of either part cannot be measured precisely. This variability and the lack of correlation between thickness of the outer layer and total enamel thickness within a sample suggests that a ratio of the two, Korvenkontio's external index, cannot be used.

At present there are few numerical data available concerning the microstructure of rodent incisor enamel. Identification of isolated incisors cannot be made on the basis of measurements alone.

DISCUSSION OF INCISOR ENAMELS

Pauciserial enamel was found by Korvenkontio to be present in ischyromyid, sciuravid, pseudosciurid, and some theridomyid

rodents. I have sectioned incisors of some of the same Eocene species; these and thin sections of different ischyromyid and sciuravid species reveal pauciserial enamel. *Prosciurus relictus,* a mid-Oligocene ischyromyid has uniserial enamel. Korvenkontio found a condition transitional between pauciserial and uniserial in the Oligocene theridomyid, *Nesokerodon minor.*

Completely uniserial and multiserial enamels are first met with in incisors of early Oligocene rodents. Korvenkontio found uniserial enamel in species of this age in the Theridomyidae and Ischyromyidae, and I have observed it in *Cylindrodon fontis* of the Cylindrodontidae. Other species having uniserial enamel are listed in Table 5.

Multiserial enamel is characteristic of all caviomorph rodents so far examined. Wood and Patterson (1959: 292)[2] found it in a Deseadan (early Oligocene) incisor, very probably of *Scotamys antiquus,* and I have found it in *Cephalomys arcidens* from deposits of the same age. The early Oligocene African phiomyid rodents sectioned by me had acquired multiserial enamel; thin sections of incisors of *Phiomys andrewsi, Metaphiomys schaubi,* and a new species (Wood, in press) demonstrate this. The Recent *Thryonomys* and *Petromus,* which Lavocat (1962) and Wood (in press) associate closely with the phiomyids, also prove to have multiserial enamel. Other species possessing multiserial enamel are listed in Table 5.

Pauciserial enamel is a good structural predecessor for uniserial and multiserial enamels. It would appear to be the ancestral condition. As far as present evidence goes, it had probably been achieved by the time rodents made their first appearance in the record. It is known thus far in only a few post-Eocene rodents, and uniserial and multiserial enamels have not yet been recorded prior to the Oligocene. Presumably acquisition of two layers in which the organization of prisms is different served in some way to strengthen the enamel. The pauciserial structure, judging from the record, would appear to have been less efficient than the other two. There is no available evidence to suggest that one of the two surviving kinds is superior to the other or that one of them has ever evolved from the other. Seemingly, selection has favored increase in strengthening rather than any one method of accomplishing it.

To the possible question: could the pauciserial condition be an artifact caused by diagenetic changes in materials of greater age?

[2] A lapsus in this paper may be corrected. The authors state (p. 292 n.): ". . . the Theridomyidae are in the process of passing from a pauciserial to a multiserial type." For "multiserial" read "uniserial."

I would reply in the negative. In none of the many slides of enamel of Eocene age that I have examined is there any indication that recrystallization has disrupted the fine structure.

The enamels of all modern rodent incisors fall into one of the two major categories, uniserial and multiserial, but there are minor differences within each of the two as regards dimensions and orientation of lamellae. Study of the internal detail of lamellar structure is needed to understand the differences and to determine how they may have evolved.

ACKNOWLEDGMENTS

I began this research at Amherst College and received support in 1964-65, through the Geology Department, from the Student Research Participation Program of the National Science Foundation. The work was continued in the summer of 1965 under Public Health Service Grant 2 TI GM 306-06 to the Biology Department of Amherst College, and other help was forthcoming from National Science Foundation Grant GB 1977 to Professor Albert E. Wood. I am indebted to Professor Wood and to Professor Bryan Patterson for their guidance, and to Miss Barbara Lawrence and Mr. Charles Mack of the Mammal Department, Museum of Comparative Zoology, for permitting me to section various specimens.

TABLE 5

Enamel structure in rodent incisors.

The initials after each species name are those of the authors who have described its incisor enamel. Species names are mainly as in Ellerman (1941); familial and generic assignments are mainly as in Simpson (1945). Where a name given in the publications of those who have described rodent incisor enamels differs from the current one, I have included it in brackets. A classification of rodents above the familial level is given by Wood (1958)

Abbreviations: B., Bohlin (1946); K., Korvenkontio (1934); T., Tomes (1850); W., Wahlert; W. and P., Wood and Patterson (1959). Eoc., Eocene; Olig., Oligocene; Mioc., Miocene; Pleist., Pleistocene; E., early; M., mid; L., late. Af., Africa; As., Asia; Eu., Europe; N.A., North America; S.A., South America. (Geologic age and location given only for fossils.)

PAUCISERIAL ENAMELS

Ischyromyidae: *Ischyrotomus petersoni* W., L.Eoc. N.A. *Knightomys depressus* W., E.Eoc. N.A. *Manitsha* sp. W., E.Olig. N.A. *Microparamys tysitensis* W., E.Eoc. N.A. *Paramys c. copei* K., W., E.Eoc. N.A. *Paramys*

c. major K., W., E.Eoc. N.A. *Paramys delicatior* K., M.Eoc. N.A. *Paramys excavatus* K., W., E.Eoc. N.A. *Thisbemys perditus* W., E.Eoc. N.A.

Sciuravidae: *Mysops parvus* W., M.Eoc. N.A. *Sciuravus nitidus* K., M.Eoc. N.A.

Theridomyidae: *Archaeomys gracilis* K., L.Eoc.-M.Olig. Eu. *Archaeomys major* K., L.Eoc.-M.Olig. Eu. *Theridomys gregarius* K., L.Eoc.-M.Olig. Eu. *Theridomys vaillanti* K., Eoc. Eu.

Pseudosciuridae: *Pseudosciurus suevicus* K., E.Olig. Eu. *Sciuroides quercyi* K., L.Eoc.-M.Olig. Eu. *Sciuroides* sp. K., L.Eoc.-M.Olig. Eu.

UNISERIAL ENAMELS

Ischyromyidae: *Ischyromys typus* K., M.Olig. N.A. *Prosciurus relictus* W., M.Olig. N.A. *Titanotheriomys veterior* K., E.Olig. N.A.

Cylindrodontidae: *Cylindrodon fontis* W., E.Olig. N.A.

Aplodontidae: *Allomys nitens* K., L.Olig. N.A. *Aplodontia rufa* K.

Mylagaulidae: *Mesogaulus novellus* W., M.Mioc. N.A. *Mylagaulus* sp. W., L.Mioc. N.A.

Muridae: *Acomys* sp. K. *Arvicanthis* sp. K. *Conilurus [Hapalotis] albipes* T. *Hydromys chrysogaster* T. *Mus. musculus* K. *Notomys [Hapalotis] longicaudatus* T. *Otomys* sp. K. *Rattus norvegicus [Mus decumanus* T., K.*]* T., K., W. *Rattus [Mus] rattus* K.

Cricetidae: *Cricetodon minor* K., L.Mioc. Eu. *Eumys elegans* K., W., M.-L.Olig. N.A. *Eumys gracilis* K., Olig. N.A. *Sigmodon* sp. W., L.Pleist. N.A. *Akodon arenicola* K. *Arvicola amphibius* T. *Arvicola [Microtus] terrestris* K. *Clethrionomys [Arvicola* T., *Evotomys* K.*] glareolus* T., K. *Cricetulus migratorius [phaeus]* K. *Cricetus cricetus [fumentarius* T.*]* T., K. *Ellobius talpinus* K. *Gerbillus* sp. K. *Lemmus lemmus [norvegicus]* T., K. *Meriones [Gerbillus] shawi* T. *Microtus [Arvicola] nivalis* T. *Myopus schisticolor* K. *Ondatra [Fiber] zibethica* T., K. *Oryzomys flavescens [longicaudatus]* K. *Oxymycterus rufus* K. *Phyllotis [Hesperomys] darwinii* T. *Tatera* sp. K.

Spalacidae: *Spalax microphthalmus [typhlus]* T., K. *Tachyoryctes splendens* K.

Geomyidae: *Entoptychus cavifrons* K., E.Mioc. N.A. *Entoptychus* sp. K., L.Olig. N.A. Entoptychine geomyid W. M.Mioc. N.A. *Heterogeomys hispidus* K. *Thomomys [Geomys] umbrinus* T.

Heteromyidae: Heteromyid W., M.Mioc. N.A. *Dipodomys* sp. K. *Perognathus fasciatus* K. *Perognathus* sp. K. *Perognathus [Cricetodipus]* sp. K.

Eomyidae: *Adjidaumo* sp. W., M.Olig. N.A. *Paradjidaumo trilophus* W., M.Olig. N.A.

Dipodidae: *Alactaga sibirica [saliens]* K. *Jaculus jaculus [Dipus hirtipes]* K. *Jaculus [Jerboa* T., *Dipus* K.*] orientalis [aegyptius]* T. K.

Zapodidae: *Napaeozapus insignis* K. *Sicista [Sminthus] subtilis* K. *Zapus hudsonius* K.

Gliridae: *Glis [Myoxus] wetzleri* K., L.Olig. Eu. *Dryomys nitedula* K. *Eliomys quercinus* K. *Glis [Myoxus* K.*] glis* K., W. *Graphiurus ocularis [capensis]* K. *Muscardinus [Myoxus* T.*] avellanarius* T., K.

Sciuridae: *Sciurus feignouxi* K., E.Mioc. Eu. *Callosciurus [Sciurus] prevosti* K. *Citellus [Spermophilus] eversmanni* K. *Citellus parryii [Spermophilus empetra]* K. *Citellus [Spermophilus]* sp. T. *Cynomys ludovicianus* K. *Marmota caligata [Arctomys pruinosus]* T. *Marmota [Arctomys] monax [empetra* T.*]* T., K. *Marmota [Arctomys* K.*]* sp. K., W. *Petaurista volans [Pteromys russicus]* K. *Ratufa [Sciurus] macroura* K. *Sciurus niger* T. *Sciurus vulgaris* K. *Tamias sibiricus [Eutamias asiaticus]* K. *Tamias striatus [lysteri* T.*]* T., K.

Castoridae: *Steneofiber eseri* K., E.Mioc. Eu. *Steneofiber peninsulatus* K., L.Olig. N.A. *Castor fiber* T., K.

Eutypomyidae: *Eutypomys thomsoni* W., M.Olig. N.A.

Theridomyidae: *Archaeomys laurillardi* K., Olig. Eu. *Nesokerodon minor* K., L.Eoc.-M.Olig. Eu. *Sciuromys typicus* K., L.Eoc.-M.Olig. Eu.

Anomaluridae: *Anomalurus fraseri* K. *Idiurus macrotis* K.

MULTISERIAL ENAMELS

Octodontidae: *Sciamys principalis* K., E.Mioc. S.A. *Aconaemys [Schizodon] fuscus* T. *Octodon degus* T. *Spalacopus cyanus [poeppigii]* T.

Echimyidae: *Adelphomys candidus* K., E.Mioc. S.A. *Myocastor [Myopotamus* T.*] coypus* T. K.

Ctenomyidae: *Ctenomys magellanicus* K.

Abrocomidae: *Abrocoma [Habrocoma] bennettii* T.

Capromyidae: *Capromys pilorides [fournieri]* T.

Chinchillidae: *Scotamys antiquus* W. and P., E.Olig. S.A. *Perimys procerus* K., E.Mioc. S.A. *Chinchilla laniger* T. *Lagostomus maximus [trichodactylus]* K.

Dasyproctidae: *Cephalomys arcidens* W., E.Olig. S.A. *Neoreomys australis* K., E.Mioc. S.A. *Cuniculus [Coelogenys] paca* T., K. *Dasyprocta aguti* T., K. *Myoprocta [Dasyprocta] acouchy* T.

Caviidae: *Cavia aperea* T. *Cavia porcellus [cutleri]* K. *Dolichotis patagona* K. *Galea [Kerodon] flavidens* K. *Galea [Kerodon] spixii* K. *Microcavia australis [Cavia kingii]* T.

Hydrochoeridae: *Hydrochoeris hydrochaeris [capybara]* T.

Erethizontidae: *Coendou [Hystrix* T.*] prehensilis* T., K. *Erethizon dorsatum* K. *Erethizon epixanthum* K.

Ctenodactylidae: *Sayimys obliquidens* B., ?Mioc. As. *Tataromys* cf. *plicidens* B., ?Mioc. As. *Ctenodactylus gundi* K., B.

Pedetidae: *Pedetes cafer* T., K.

Hystricidae: *Atherurus africanus* K. *Hystrix cristata* T.

Phiomyidae: *Metaphiomys schaubi* W., E.Olig. Af. *Phiomys andrewsi* W., E.Olig. Af. Phiomyid W., E.Olig. Af.

Thryonomyidae: *Thryonomys* sp. W.

Petromuridae: *Petromus typicus* W.

Bathyergidae: *Bathyergus suillus [maritimus]* T. *Cryptomys mellandi* K. *Georychus capensis* K.

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(Received 15 August 1968.)